REPRODUCTIVE POTENTIAL OF FEMALE EASTERN BERING SEA TANNER CRAB

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Abstract

Changes in abundance and sex ratio can contribute to variation in the reproductive potential of a population. The commercially important Bering Sea Tanner crab (*Chionoecetes bairdi*) are distributed throughout the north Pacific Ocean and display cyclical population dynamics. The goal of this study was to examine how fishing pressures and population dynamics affected the reproductive potential of Bering Sea Tanner crab to better inform sustainable fishery management. I quantified female stored sperm levels and fecundity for both primiparous (in their first reproductive cycle) and multiparous (in their second or later reproductive cycle) crab to examine spatial and temporal variation in reproductive potential. Multiparous female crab had higher spermathecal load than primiparous ones, but spermathecal load varied widely across female size. Higher sperm cell counts were associated with visual indication of fresh ejaculate for primiparous crab but not for multiparous crab. Sperm cell counts increased with increasing spermathecal load for both primiparous and multiparous crab, although the slope of the regression line varied for the two categories. Female fecundity was highest in crab in their second year after the terminal molt to maturity and was lower in the first year and in the third and subsequent years. Female fecundity (size-corrected) did not differ among management areas. Measures of mature female sperm storage and quantification of reproductive stage can provide fishery managers with an early warning of reproductive failures.

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Introduction

An understanding of the reproductive potential of a population can be useful to develop biological reference points or data-informed model parameters to sustainably manage a fished stock. Knowledge of recruitment of juvenile individuals to a population allows biologists to better predict shifts in population abundance (Zheng and Kruse 2006). Investigation of variability in reproductive potential may provide insight into recruitment dynamics and information on sustainable harvest levels by allowing managers to better predict when populations are approaching levels that could allow reproductive failures.

For many crustacean fisheries, the selective removal of large males from the population can affect reproductive success (Millikin and Williams 1984; Rondeau and Sainte-Marie 2001; Sato et al. 2007; Sato and Yoseda 2010; Sato 2012; Pardo et al. 2015, 2017), including altering the operational sex ratio and reducing reproductive potential through a decrease in the quantity of sperm delivered during mating (Lovrich et al. 1995; Rondeau and Sainte-Marie 2001; Sato et al. 2007; Ogburn et al. 2014; Pardo et al. 2017). For example, spiny king crab (*Paralithodes brevipes*) off eastern Hokkaido, Japan had a higher proportion of empty or incomplete clutches in heavily fished years compared to years with lower fishing pressure (Sato et al. 2007). Further, decreased sperm storage in males and reduced sperm reserves and embryo production in females is associated with heavy fishing pressures for southern rock crab (*Metacarcinus edwardsii*) (Pardo et al. 2015, 2017). The decrease in male sperm storage was due primarily to differences in number of spermatophores as opposed to decreases in other seminal material (Pardo et al. 2015). Similar negative results of large male only harvest can be seen in other decapod crustaceans, including coconut crab *Birgus latro* and stone crab *Hapalogaster dentata* (Sato and Yoseda 2010; Sato 2012). When population sex ratios of snow crab (*Chionoecetes opilio*), a congener of

Tanner crab (*C. bairdi*), become biased towards females, males allocate lower amounts of sperm per mating in order to preserve sperm for future matings (Rondeau and Sainte-Marie 2001).

Snow crab in the Gulf of Saint Lawrence and the Bering Sea inhabit varying depths according to size and condition, which has implications for mating dynamics and reproductive success (Lovrich et al. 1995; Zheng et al. 2001; Murphy et al. 2011). Smaller males move to shallower depths in sync with pubescent females, while larger males remain at greater depths and mate with multiparous females (Lovrich et al. 1995; Zheng and Kruse 2003; Murphy et al. 2011). When larger males are removed from the population, multiparous females may experience limited mating opportunities (Rondeau and Sainte-Marie 2001; Sato 2012). Multiparous females in the Bering Sea are more fecund than females reproducing for the first time (Webb et al. 2016) and thus are important for the overall reproductive success of the population. This complex mating behavior is much better understood for snow crab than for Tanner crab (*C. bairdi*), even though both are important and overlapping commercial fisheries in the Bering Sea.

Tanner crab are distributed primarily in the eastern Pacific Ocean ranging from Oregon in the south to the Aleutian Islands and eastern Bering Sea (EBS) in the north, but are also found in the western Pacific Ocean near Kamchatka (Donaldson and Adams 1989). Within Alaska they are distributed from Southeast Alaska through the Gulf of Alaska and into the southeastern Bering Sea. The northern extent of Tanner crab overlaps with the southern extent of snow crab, and the two species can hybridize (Jadamec et al. 1999).

Tanner crab growth occurs through molting. They molt often during their first 2 years after settlement (Donaldson et al. 1981), and they continue to molt until they reach maturity at a final terminal molt (Hilsinger 1976, Donaldson and Adams 1989, Tamone et al. 2007). Females

reach maturity at about five years of age, and males reach maturity at about six years of age (Donaldson and Adams 1989). There is currently no accepted method for determining the age of Tanner crab, as the hard structures that have been proposed for age determination have not been demonstrated to be retained through molting (Vogt 2012; Kilada et al. 2017; Crook et al. 2018). The inability to accurately age Tanner crab has led biologists to estimate the relative wear and growth of epibionts on the crab exoskeleton to create categories of shell condition (SC) that serve as a proxy for time since terminal molt (Jadamec et al. 1999). Additionally, SC corresponds with female reproductive status. Crab that molted recently, have a shell relatively clean of epibionts, and lack grasping marks (SC1 or SC2) are assumed to be in their first reproductive cycle and are termed primiparous. Crab with visible wear on the exoskeleton, epibionts on their shell, and grasping marks on the dactyls from mating in hardshell condition (SC3 or higher), are assumed to be in their second or subsequent reproductive cycle.

Tanner crab mating occurs during two overlapping periods in winter and early spring (Donaldson and Adams 1989; Stevens et al. 1993, 1994). Tanner crab females mate for the first time soon after the terminal molt to maturity and are able to store sperm in internal sperm storage organs until it is needed for fertilization of oocytes (Donaldson and Adams 1989; Duluc et al. 2005). Females extrude embryos and brood their clutch externally under their abdominal flap on an annual cycle (Donaldson and Adams 1989; Paul and Paul 1992; Webb 2009). Embryos hatch in the spring and females either mate again or use stored sperm to fertilize their subsequent clutch (Donaldson and Adams 1989; Stevens 2003; Swiney 2008). *In situ* observations of Tanner crab mating showed pubescent females mating in shallower water with primarily smaller males while multiparous females mated in deeper water with larger males. In at least some instances,

multiparous females also aggregate in large numbers at the time of larval release and are likely able to choose whether to mate with available males (Stevens et al. 1993, 1994).

Female sperm storage has been hypothesized to provide a reproductive buffer, in which heavy fishing on large males may have less impact on reproductive output (Slater et al. 2010). Tanner crab can fertilize at least two sequential annual egg clutches using only stored sperm (Paul 1984; Paul and Paul 1992), but the total length of time that stored sperm remains viable is unknown (Adams et al. 1983). In laboratory studies that deny females access to a mate before their second reproductive cycle, approximately half or more of the females had not stored enough sperm to produce a full and viable second clutch (Paul and Paul 1992; Webb 2009). If the female is in a soft state during copulation (i.e., immediately following molt to maturity), it is possible for her to mate with males up to 30 mm smaller in carapace width (CW); however, if the female is not flaccid from a recent terminal molt, the male must be of equivalent or greater size for the mating to be successful (Donaldson and Adams 1989). In captivity, male *Chionoecetes* crab are capable of mating twice in the same day or several times within a week with no significant difference in the amount of sperm transferred during mating (Adams et al. 1983; Sainte-Marie and Lovrich 1994). The size of the male mate does not have any clear effect on amount of sperm transferred to the female (Adams et al. 1983); however, larger males typically dominate when mating is contested (Stevens et al. 1993).

Tanner crab fecundity estimates range from 24,000 to 318,000 embryos per clutch (Hilsinger 1976). Primiparous females (i.e., those in their first reproductive cycle) tend to have lower fecundity than multiparous females (i.e., those in their second or subsequent reproductive cycle; Somerton and Meyers 1983). Additionally, fecundity is significantly correlated with maternal characteristics such as carapace width (Webb and Bednarski 2009).

The Bering Sea Tanner fishery has exhibited large swings in harvest. The first reports of incidental harvest of Tanner crab from the EBS occurred in 1968 (Fitch et al. 2010). After the first directed fishery in 1974, Bering Sea Tanner crab became an economically important fishery, annually worth an average of $16 million (USD) between 1979 and 2011 (Fitch et al. 2010). Catch declined from a peak harvest of 30,200 t (66.6 million pounds) in the 1977/78 season to 548.0 t (1.2 million pounds) by 1984/85 (Figure 1; Fitch et al. 2010; Stockhausen 2019). Since 1995, the catch and survey abundance have been much lower than during peak years. The stock was declared overfished in 1998 and 2010, and the fishery was closed due to low abundance for 8 years beginning in 1996/97 as well as 3 seasons beginning in 2006/07 (Fitch et al. 2010; Stockhausen 2019) and the 2016/17 season (Stockhausen 2019). The total retained catch from the 2018/19 season was 1,100 t (2.5 million pounds; Figure 1; Stockhausen 2019).

Commercial crab fisheries in the EBS are managed under a state-federal cooperative regime established in the North Pacific Fisheries Management Council (NPFMC) Fishery Management Plan (FMP) for Bering Sea/Aleutian Islands King and Tanner crab (NPFMC 2011). Regulations set by the Alaska Department of Fish and Game (ADF&G) restrict harvest to males of a minimum legal size with total harvest not to exceed Total Allowable Catch (TAC) limits. These limits are set separately for the areas east and west of longitude 166 °W in the EBS, although there is little evidence that the EBS contains two distinct, non-interbreeding stocks (Stockhausen 2019). Under the FMP, the annual Bering Sea Tanner crab TAC established by ADF&G must prevent total fishery mortality from exceeding the Acceptable Biological Catch (ABC) established annually by the NPFMC stock assessment.

To ensure a sustainable population and fishery, the primary management objective is to maintain the long-term reproductive viability of crab stocks (NPFMC 2011). Mature male

biomass at the time of mating is currently used as an index of spawning stock biomass for EBS Tanner crab stock assessment (Stockhausen 2019). However, the Scientific and Statistical Committee of the NPFMC recommended that research is needed to develop measures of spawning stock biomass that consider the dominant role of females in reproduction (NPFMC 2013). Currently, the only consideration for female biomass is a control rule in the State of Alaska harvest strategy that triggers fishery closures or reductions in TAC according to the ratio of current female biomass to the average historical female biomass (5 AAC 35.508[5]). Additionally, the NPFMC has identified research on quantitative methods of assessing reproductive success as a central research need for fishery management. Specifically, research on sperm reserves and fecundity of female EBS Tanner crab is needed for incorporation into the stock assessment process and to understand the effects of sex ratios, stock distribution, and environment on stock productivity (NPFMC 2013).

The goal of this project was to identify factors that influenced female fecundity and sperm reserves. I aimed to describe functional relationships among maternal characteristics, such as reproductive status (SC), size (CW), spatial area, sperm reserves, and fecundity. Specifically, I investigated female sperm storage as a function of female size, compared spermathecal load and sperm cell count between primiparous and multiparous crab and between spatial area east and west of longitude 166 °W, and evaluated if visual presence of a fresh ejaculate layer in the spermatheca was associated with an increased sperm cell count. Additionally, I evaluated the relationship between sperm cell counts and spermathecal load, which could drastically decrease processing time for sperm reserve quantification by eliminating the need to count intact sperm

[5] Alaska Administrative Code: Bering Sea District C. *bairdi* Tanner crab harvest strategy

cells. Finally, I compared female fecundity east and west of longitude 166 °W and examined relative change in female fecundity with changes in shell condition.

Methods

Mature female Tanner crab were opportunistically collected from the EBS during the National Oceanic and Atmospheric Administration Resource Assessment and Conservation Engineering trawl survey using an 83-112 eastern otter trawl (Weinberg 2003) during 2007-2015 (Figure 2). Crab were either frozen, held live in flow through tanks on deck, or preserved in formalin. After completion of the survey, crab were transported to either Kodiak or Juneau for processing. Live crab were held in flow-through seawater tanks and fed a diet of shrimp, herring, and squid twice a week.

During processing, several external measures of female crab were recorded, including carapace width (CW), disease presence, and shell condition (Jadamec et al. 1999), and then females were sampled for fecundity and dissected to remove the spermathecae. Crab with a shell condition score of 1 or 2 were defined as primiparous, score 3 were defined as multiparous and score 4 or higher were defined as old multiparous. To assess fecundity, the abdominal flap was removed from the female and embryos were separated from the pleopods. Two replicate embryo subsamples were counted to estimate fecundity, according to procedures by Webb (2009). Fecundity was quantified for 1,153 females (Table 1). Spermathecae were evaluated for the presence of fresh ejaculate, measured as a white layer of material located at the ventral end of the spermathecae (Duluc et al. 2005), and overall spermathecae fullness. If the spermathecae appeared identical, one spermatheca was designated the primary spermatheca (default right if intact) and placed in 10% buffered formalin for future processing. The remaining spermatheca, if intact, was designated as secondary and placed in formalin for every alternating crab. If there

were differences in the shape or amount of material in the spermathecae, both were treated as primary samples. After spermathecae remained in formalin for at least one week, the epithelial layer was removed and contents were weighed, defined here as spermathecal load, for a total of 821 crab (Table 2). The contents were then cut in half longitudinally and the number of layers counted. Layers were aged according to the color and consistency of the material. The material in the primary spermatheca was then macerated to break up spermatophore packets and diluted to a known quantity. The number of sperm cells in 2 x 10^{-5} ml of solution were counted on a hemacytometer in replicate and the quantity extrapolated to the total volume of the solution (Webb 2009) for 228 crab (Table 2). The contents in one spermatheca can be used to approximate the amount of contents in the other spermatheca as the sperm is generally balanced between the pair (Sainte-Marie and Lovrich 1994); therefore, all sperm cell counts were doubled to approximate the total number of sperm cells in both spermathecae, and the spermathecal load was doubled if only one spermatheca was processed.

Variability in spermathecal load, sperm cell counts, and fecundity by female size, female reproductive stage, and spatial area (east and west of longitude 166 °W), as well as the relationship between spermathecal load and sperm cell count was examined using a linear mixed modeling approach to control for potential pseudo-replication created by collecting multiple females from the same station. Variability in spermathecal load by female size, female spatial area, and year was analyzed separately for primiparous and multiparous females to allow for different relationships by reproductive stage; however, models for both primiparous and multiparous females maintained the same structure. The full model structure was

$$SL^{1/3} = \alpha + a_i + a_t + \beta CW + \delta Area + \varepsilon$$

where α is the overall intercept, a_i is the random intercept for station *i*, a_t is the random intercept for year *t*, β is the change in spermathecal load with a unit change in female carapace width, δ is the effect of area (where 'area' is a dummy variable that is 0 for the area east and 1 is for the area west of longitude 166 °W) and ε is a residual that is assumed to be normally distributed with means 0 and variance σ_ε^2. Spermathecal load was cube-root transformed as this transformation resulted in residuals that were approximately normally distributed. The variability in spermathecal load among years was further examined by modeling the response as a linear trend over time as $SL^{1/3} = \alpha + a_i + \beta Year + \varepsilon$ where α, a_i, and ε are as above and β is the average annual change in spermathecal load. Variability in spermathecal load by ontogeny was analyzed using the full model structure $SL^{1/3} = \alpha + a_i + a_t + \gamma RS + \varepsilon$ where α, a_i, a_t, and ε are as above and γ is the effect of reproductive stage and RS is a dummy variable that is 0 for primiparous and 1 for multiparous females. Variability in sperm cell counts was also modeled separately for primiparous and multiparous females. To analyze variability in sperm cell count by area and presence of fresh ejaculate the full model structure $SCC^{1/3} = \alpha + a_i + \delta Area + \partial FE + \varepsilon$ was used where α, a_i, δ, and ε are as defined above, and ∂ is the effect of visual detection of fresh ejaculate in the spermathecae, and FE is a dummy variable that is 0 fresh ejaculate was not visually detected and 1 when fresh ejaculate was visually detected. Like spermathecal load, sperm cell count was cube-root transformed as this resulted in an approximate normal distribution of the residuals. The model structure for analyzing differences in sperm cell count by reproductive stage was $SCC^{1/3} = \alpha + a_i + \gamma RS + \varepsilon$. Year was not included as a fixed effect or random intercept term in the sperm cell count methods due to the low number of years with available data (Table 2). To analyze the relationship between sperm cell count and spermathecal load a model of the form $SCC^{1/3} = \alpha + a_i + \beta SL^{1/3} + \varepsilon$ was used where α, a_i,

and ε are as defined above and β is the change in sperm cell count with spermathecal load. Variability in fecundity was analyzed using two hurdle models to control for natural zeroes in the data. The binomial component of these models estimates the probability of a female producing a clutch of embryos and the gaussian component models variability in the number of embryos a female produces if she does produce embryos. The first hurdle model was fit separately for primiparous and multiparous females. The binomial component of this model had the structure $log(\frac{p}{1-p}) = \alpha + a_i + a_t + \beta CW + \gamma Area + \varepsilon$ where p is the probability that a clutch is produced, log $(\frac{p}{1-p})$ is the log-odds ratio, and all other parameters are as defined above. The Gaussian component had the structure $fecundity^{1/2} = \alpha + a_i + a_t + \beta CW + \gamma Area + \varepsilon$. The second hurdle model analyzed variability in female fecundity by shell condition. The binomial component had the structure $log\ (\frac{p}{1-p}) = \alpha + a_i + a_t + \beta CW + \gamma SC + \varepsilon$ where p, log $(\frac{p}{1-p})$, α, a_i, a_t, β, and ε are defined as above and γ is the effect of shell condition where SC is a dummy variable that is 0 for shell condition 2, 1 for shell condition 3, and 2 for shell condition 4. The Gaussian component had the structure $fecundity^{1/2} = \alpha + a_i + a_t + \beta CW + \gamma SC + \varepsilon$. Models were fit using a square-root, cube-root, and log transformation of fecundity and the square-root transformation was selected as it resulted in the best approximation of normally- distributed residuals. All statistical analyses were implemented using the program R (R Core Team 2019). Mixed effect models were constructed using R packages nlme (Pinheiro et al. 2018) and lme4 (Bates et al. 2015). Post-hoc pairwise analysis on the variability of fecundity by shell condition was performed using the package emmeans (Lenth 2019). Homogeneity of variance was confirmed by utilizing the Brown-Forsyth test, and normality of model residuals confirmed through visual inspection of normal-quantile plots and QQ correlation coefficient tests. Normality transformations were compared through visual observation of data spread and visual

observations of residual plots. Tanner crab populations have cyclical recruitment pulses, which makes certain reproductive stages dominate the population in particular years (Figure 3) and causes unbalanced numbers of samples for a particular reproductive stage across years. Therefore, interannual differences in the response may be confounded with differences among reproductive stage. Where possible, this was addressed by analyzing reproductive stages independently but could not be controlled for in analyses which include both reproductive stages. The statistical significance of individual effects (covariates) was assessed using the package lmerTest (Kuznetsova et al. 2017).

Results

Model estimated mean spermathecal load was 41% higher for multiparous compared to primiparous crab ($p<0.001$, Appendix A; Figure 4; Table 3). Spermathecal load was not significantly related to carapace width for either primiparous or multiparous crab ($p=0.810$ for primiparous crab, $p=0.393$ for multiparous crab, Appendix A; Figure 4; Table 3). Spermathecal load was not significantly different in the area east of longitude 166 °W compared to the area west of longitude 166 °W for primiparous females ($p=0.786$, Appendix A; Figure 4) but model estimated mean was 0.057 g lower in the west for multiparous females ($p=0.034$, Appendix A; Figure 4; Table 3) although the comparison suffered from a small sample size (Table 2). When considering year as a continuous variable, there was a decrease in spermathecal load of 0.007 g per year time for primiparous females ($p=0.033$, Appendix A; Figure 5). No significant change over time was detected for multiparous females ($p=0.455$, Appendix A; Figure 5).

Model estimated mean sperm cell counts were 22% lower for multiparous than for primiparous crab ($p<0.001$, Appendix A; Figure 6; Table 3). Visual indication of fresh ejaculate was found in 74% of primiparous crab and 87% of multiparous crab. The mean sperm cell count

of primiparous crab with fresh ejaculate was 60% higher than for crab without fresh ejaculate ($p<0.001$, Appendix A; Figure 6; Table 3), but no significant difference was detected for multiparous crab at the $\alpha=0.05$ level ($p=0.075$, Appendix A; Figure 6; Table 3). Sperm cell count was significantly higher for primiparous crab in the area east of longitude 166 °W than the area in the west ($p=0.011$, Appendix A; Figure 6; Tables 2-3). There was no difference by area detected for multiparous crab ($p=0.838$, Appendix A; Figure 6; Table 3). For both primiparous and multiparous crab, sperm cell counts increased with spermathecal load ($p<0.001$ for primiparous crab and $p<0.001$ for multiparous crab, Appendix A; Figure 7; Table 3).

Mean fecundity was higher for shell condition 3 compared to both shell condition 2 crab ($p<0.001$, Appendix A; Figure 8; Table 1) and shell condition 4 crab ($p<0.001$; Figure 8; Table 4). No difference in fecundity was detected between shell condition 2 and shell condition 4 crab ($p=0.959$, Appendix A; Figure 8; Table 4). No difference in the probability of a female producing a clutch of embryos or in the number of embryos produced for a given size between the areas east and west of 166°W was detected for primiparous crab (binomial component: $p=0.840$; Gaussian component: $p=0.802$, Appendix A; Figure 9; Table 4) or for multiparous crab (binomial component: $p=0.181$; Gaussian component: $p=0.138$, Appendix A; Figure 9; Table 4). Additionally, no difference was detected in the probability of a female of a given shell condition producing a clutch ($p=0.315$; Appendix A).

Discussion

Multiparous crab had higher spermathecal load, lower sperm cell counts, and higher fecundity than primiparous crab. The lower sperm cell counts in multiparous crab suggests one of two possibilities: either intact sperm cells break down over time resulting in lower density, or females use sperm cells in a higher concentration than the sperm was received resulting in buildup of the sperm matrix (Sainte-Marie et al. 2008). Regardless of the cause, managers should consider that while Tanner crab are capable of storing sperm, it is important for females to mate annually to maintain high sperm cell density. My results contrast with a similar study from Southeast Alaska, where Tanner crab sperm cell count did not vary between multiparous and primiparous crab (Webb and Bednarski 2009).

The higher fecundity in SC3 females (presumed to be multiparous) could be a product of energetics. The large amount of energy required for growth may limit the amount of energy that can be utilized for reproduction in the first year of maturity (Somerton and Meyers 1983; Tamone et al. 2007). Since no energy is utilized for growth or molting during the second year of maturity (presumably SC3), more energy can be focused towards reproduction. Alternatively, fecundity could be limited by female pre-molt size (Somerton and Meyers 1983), in which case, shell condition 2 females of a given size would have the same mean fecundity as smaller shell condition 3 females. These trends are similar to studies performed in Southeast Alaska and in the EBS (Somerton and Meyers 1983; Webb and Bednarski 2009) although the exact relationships differ. Crab in their third reproductive cycle (equal to SC 4 in this study) from southeast Alaska have embryo production intermediate to crab in their first or second reproductive cycle (Webb and Bednarski 2009). I found that there was no difference detected between SC2 and SC4 females, likely in their first or third reproductive cycle. Crab in this study produced similar

numbers of embryos to those in Southeast Alaska in their first reproductive cycles ($\bar{Y}$=118,981 vs 116,021), but fewer embryos than those in Southeast Alaska for both their second reproductive cycle ($\bar{Y}$=151,777 vs 190,373) and third reproductive cycle ($\bar{Y}$=104,432 vs 156,546; Webb and Bednarski 2009). Early EBS studies grouped SC3 and SC4 crab and found that SC2 females produce 70% as many embryos as SC3/4 crab produce (Somerton and Meyers 1983). Using similar groupings, I found that SC2 crab produced about 85% as many embryos as SC3/4 crab produce, yet no direct comparison is possible as Somerton and Meyers (1983) did not provide sample means. The decrease in embryo production between SC3 and SC4 could be indicative of reproductive senescence (Berube et al. 1999; Schwartz et al. 2003; Sharp et al. 2010).

Sperm cell counts provide more precise information about female sperm stores than spermathecal loads but are more time-consuming and may be impractical for monitoring purposes. Processing a sample for sperm cell counts can take up to one hour, while processing for spermathecal load takes approximately 10 minutes. The relatively low number of sperm cell counts performed was a limitation in my study; however, the relationship between spermathecal load and sperm cell counts suggests that monitoring spermathecal load is a viable and more efficient solution for monitoring population reproductive success. Future studies should perform more sperm cell counts over a larger span of years to bolster the relationship between spermathecal load and sperm cell count and allow for important covariates (such as year and area) to be included in the model, which was not possible with the current sample size.

Current management strategies establish separate TACs for areas east and west of 166 °W longitude. While a gradient has been detected in mean adult female size across the Bering Sea (Somerton 1981) and larval advection studies suggest multiple metapopulation subunits in the

EBS (Richar et al. 2015), I did not find evidence that size-corrected fecundity varied across this boundary. There was slight evidence that multiparous spermathecal load and primiparous sperm cell counts varied between areas east and west of 166 °W longitude, but estimated differences in sperm reserves were minimal.

The observed trend of decreased spermathecal load over time for primiparous crab warrants further exploration and could be an early warning sign, although the minimal downward trend and the amount of interannual variation (Figure 5) suggest this trend does not represent any immediate threat to stock reproduction. Other than this preliminary result, there was no indication of sperm cell limitation in this study. No difference was found in the likelihood of multiparous females producing a clutch than primiparous females despite the multiparous females exhibiting a decreased sperm cell count. Additionally, less than 1% of primiparous females had unfertilized embryos or no spermathecal load in the spermathecae suggesting that over 99% of primiparous females had access to a mate. Sperm reserves from females in this study were similar to or higher than those found in other Alaskan populations which were not observed to be sperm-limited (Webb and Bednarski 2009). Primiparous crab in this study exhibited a higher mean spermathecal load than crab in Southeast Alaska (0.10 ± 0.10 g vs. 0.04 g ± 0.01) and count of sperm cells ($6.09 \times 10^7 \pm 5.56 \times 10^7$ vs. $1.98 \times 10^7 \pm 3.14 \times 10^6$). While spermathecal load was higher for multiparous crab in this study compared to crab from Southeast Alaska (0.28 g ± 0.19 vs. 0.20 ± 0.02), sperm cell counts were similar ($2.88 \times 10^7 \pm 3.35 \times 10^7$ vs. $2.32 \times 10^7 \pm 3.52 \times 10^6$; Webb and Bednarski 2009).

It is possible that female-biased sex ratios can be exacerbated by removal of legal-sized males from the population and can impact female sperm acquisition and in extreme cases, production of fertilized eggs (Sainte-Marie et al. 2008; Webb and Bednarski 2009). However,

operational sex ratios, particularly for multiparous females, can be skewed towards females due to mating behaviors regardless of overall population ratios. Submersible dives off Kodiak, Alaska showed mating aggregations with male:female sex ratios ranging from 1:10 to 1:100 (Stevens et al. 1994). *Chionoecetes* females may be able to detect the necessity of and avoid mating when possible to avoid resulting limb loss and fatalities (Stevens et al. 1994; Rondeau and Sainte-Marie 2001). It is likely that females can sense the amount of sperm they have retained in their spermathecae and are able to determine if it is worth risking damage to mate again (Sainte-Marie 2007). As there is also evidence that multiparous females may be less polyandrous than primiparous females and are able to selectively use spermatophores (Sainte-Marie et al. 2008), the lower sperm cell reserves observed in multiparous females could be a result of females choosing not to re-mate when unnecessary and obtaining sperm from fewer males when it is necessary. Multiparous females having lower sperm cell reserves than primiparous females while simultaneously having higher fecundity at similar body size and thus potentially requiring greater sperm reserves to fertilize each clutch suggests sperm limitation could occur; however, in the nine years of monitoring that spanned a ten-fold difference in retained catch, neither sperm reserves data nor fecundity data indicated that egg production of the EBS Tanner crab stock was limited by sperm availability.

Future monitoring study designs should maximize the geographic spread of sample collection by selecting fewer females from more stations to minimize pseudo-replication. If resources are limited, focusing monitoring on primiparous females could be beneficial as they have no opportunity to use stored sperm to fertilize subsequent clutches and it has been suggested that primiparous females are more likely to not obtain enough sperm to fully fertilize their clutch (Sainte-Marie et al. 2002, 2008). Additional data could be applied to develop a

model to estimate sperm cell counts from spermathecal load. Additionally, studies that examine the relationship between sperm reserves, fecundity, population level factors such as abundance and sex ratio, and external factors such as oceanographic parameters could further identify indicators of reproductive limitation in Alaska Tanner crab stocks.

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Tables and Figures

Table 1. Numbers of clutch samples processed for fecundity by year and area.

	Area	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
Fecundity	East	126	48	4	5	42	42	52	42	42	403
	West	155	178	28	94	56	69	27	73	70	750
	Total	281	226	32	99	98	111	79	115	112	1153

Table 2. Numbers of spermatheca samples processed for each procedure by year and area.

	Area	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
Spermathecal Load	East	70	56	4	6	28	36	36	20	20	276
	West	93	131	30	108	28	53	24	41	37	545
	Total	163	187	34	114	56	89	60	61	57	821
Sperm Cell Counts	East	27	29	0	6	0	0	0	0	0	62
	West	22	33	20	91	0	0	0	0	0	166
	Total	49	62	20	97	0	0	0	0	0	228

Table 3. Descriptive statistics for crab used to analyze carapace width (mm), spermathecal load (g), and sperm cell count.

			Sperm cell count		
	Carapace Width (mm)	Spermathecal Load (g)	Overall	East of longitude 166°W	West of longitude 166°W
Primiparous					
Min	55.60	0.00	2.86×10^5	9.90×10^6	2.86×10^5
Max	107.60	0.70	2.85×10^8	2.84×10^8	1.88×10^8
n	397	397	59	7	52
Mean	85.10	0.10	6.09×10^7	1.14×10^8	5.37×10^7
SD	10.40	0.10	5.56×10^7	9.92×10^7	4.37×10^7
Multiparous					
Min	48.90	0.00	0	0	0
Max	111.10	1.71	2.37×10^8	2.37×10^8	2.11×10^8
n	424	424	169	55	114
Mean	82.23	0.28	2.88×10^7	2.94×10^7	2.86×10^7
SD	10.23	0.19	3.35×10^7	3.51×10^7	3.28×10^7

Table 4. Descriptive statistics for crab used to analyze fecundity estimates by shell condition.

	Fecundity Estimates				
	Min	Max	n	Mean	SD
Shell Condition 2	0	285,974	443	118,981	55,932
Shell Condition 3	0	401,599	523	151,777	76,174
Shell Condition 4	0	351,729	187	104,432	66,726

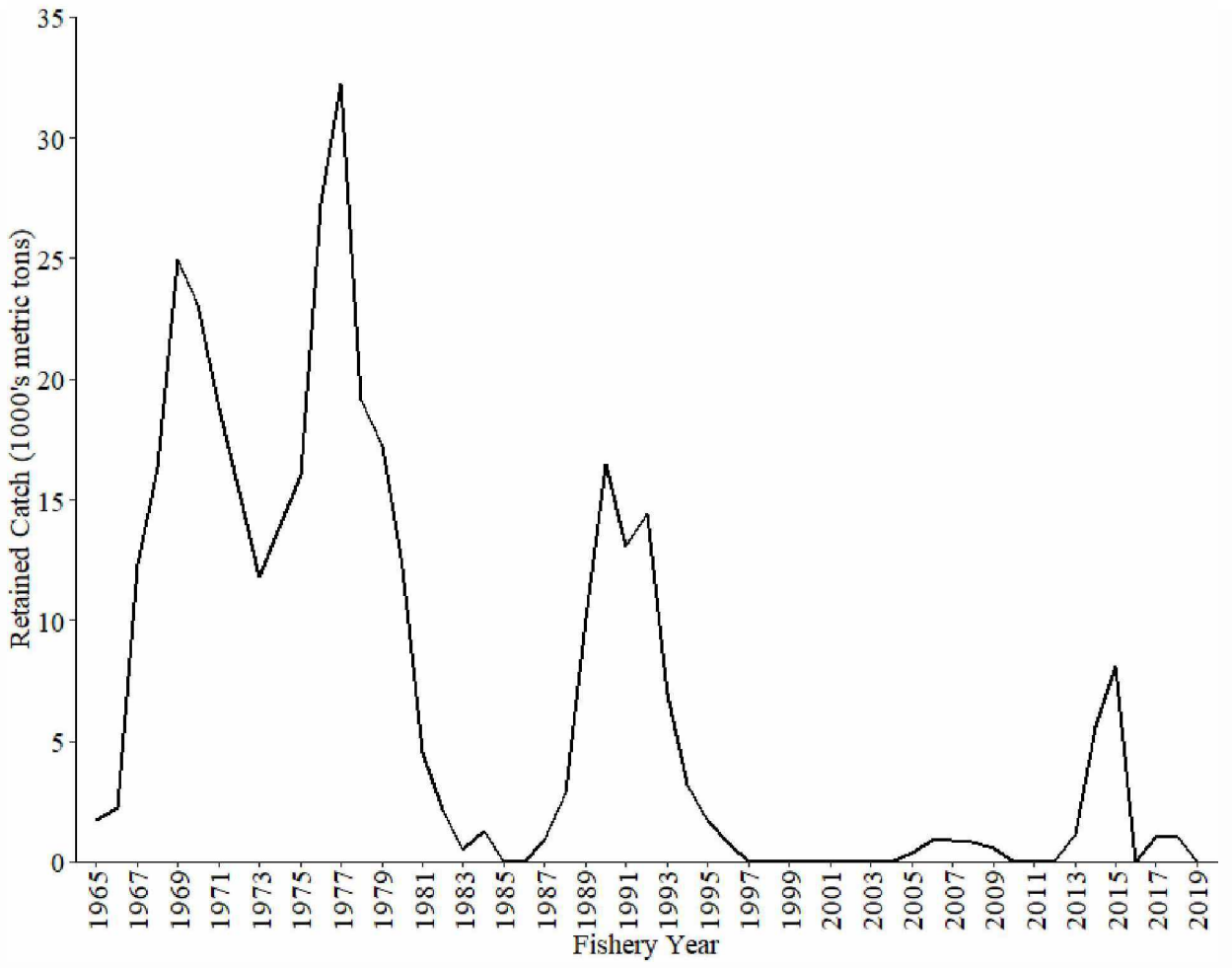

Figure 1. Retained catch of Tanner crab in the eastern Bering Sea commercial Tanner crab fishery from the 1965/66 season through the 2017/18 season. Fishery year represents the beginning year of the season (e.g., 2017 represents the season spanning from 2017 into 2018). Data obtained from Stockhausen (2018).

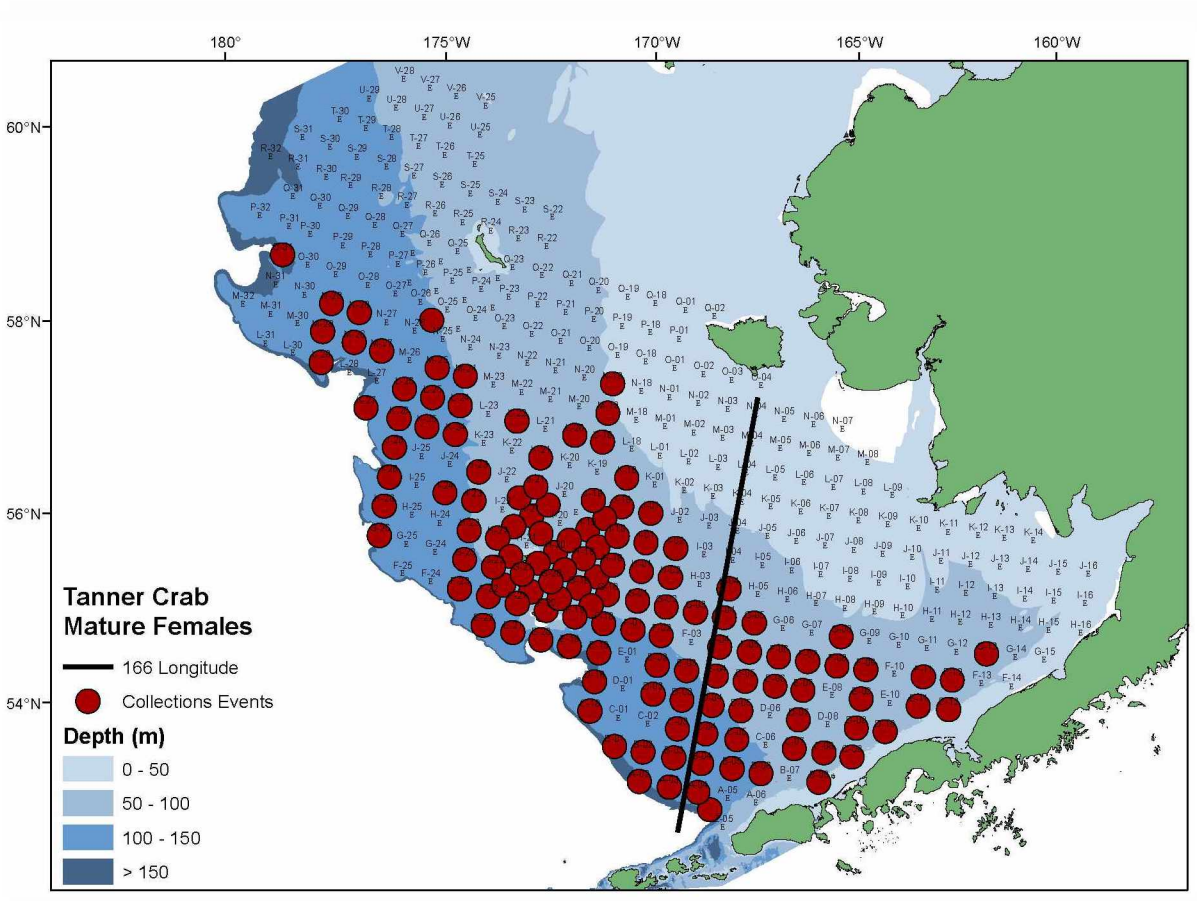

Figure 2. Locations of standard trawl survey stations and collection events for female Tanner crab from the Eastern Bering Sea (2007-2015).

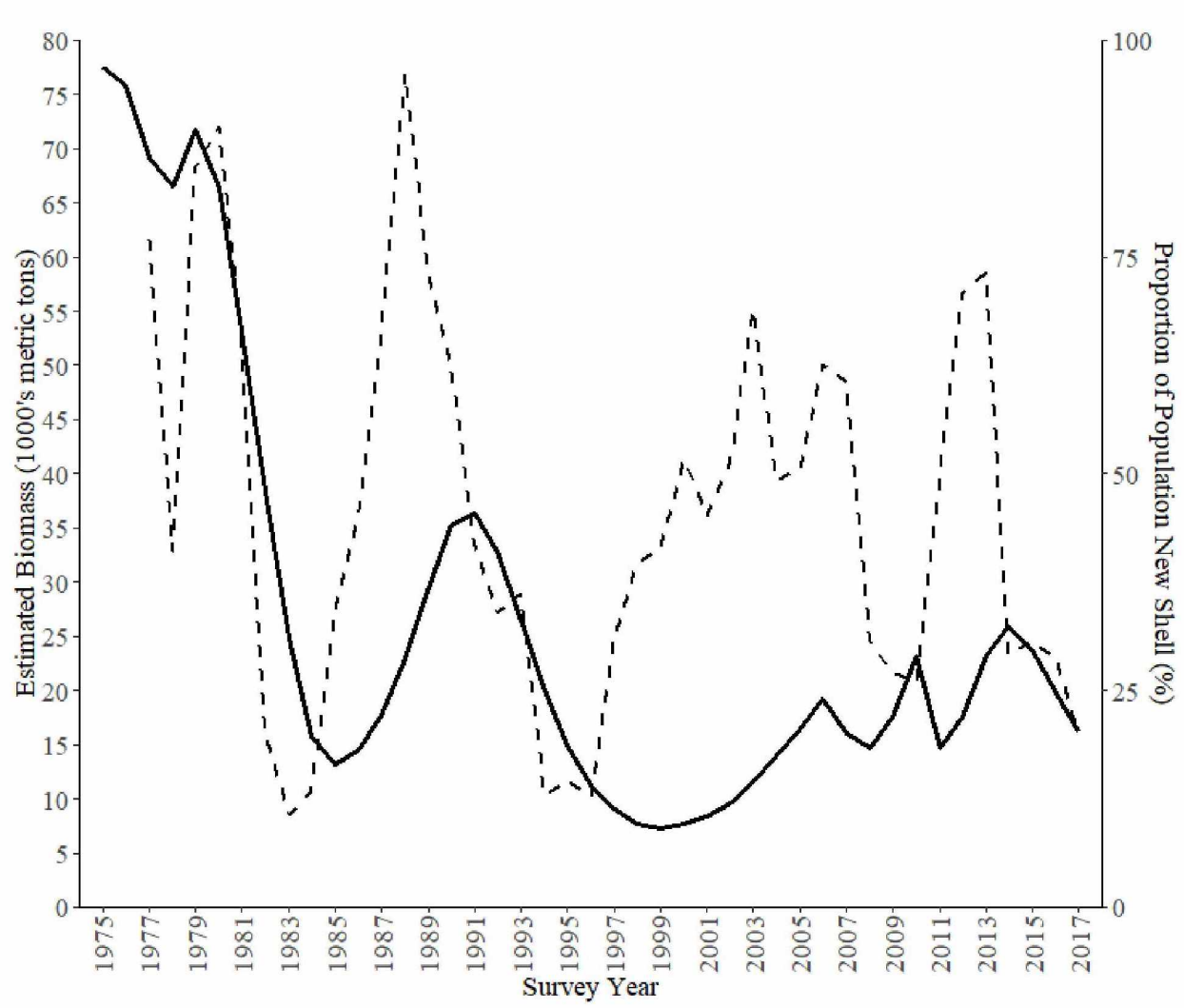

Figure 3. Estimated biomass of mature female Tanner crab from the EBS (left scale, solid line) and proportion of mature female Tanner crab from the NMFS EBS survey that are new shell (right scale, dashed line). Proportion of new shell crab appears to be partially dependent on direction of population biomass trend. Data from Stockhausen (2018).

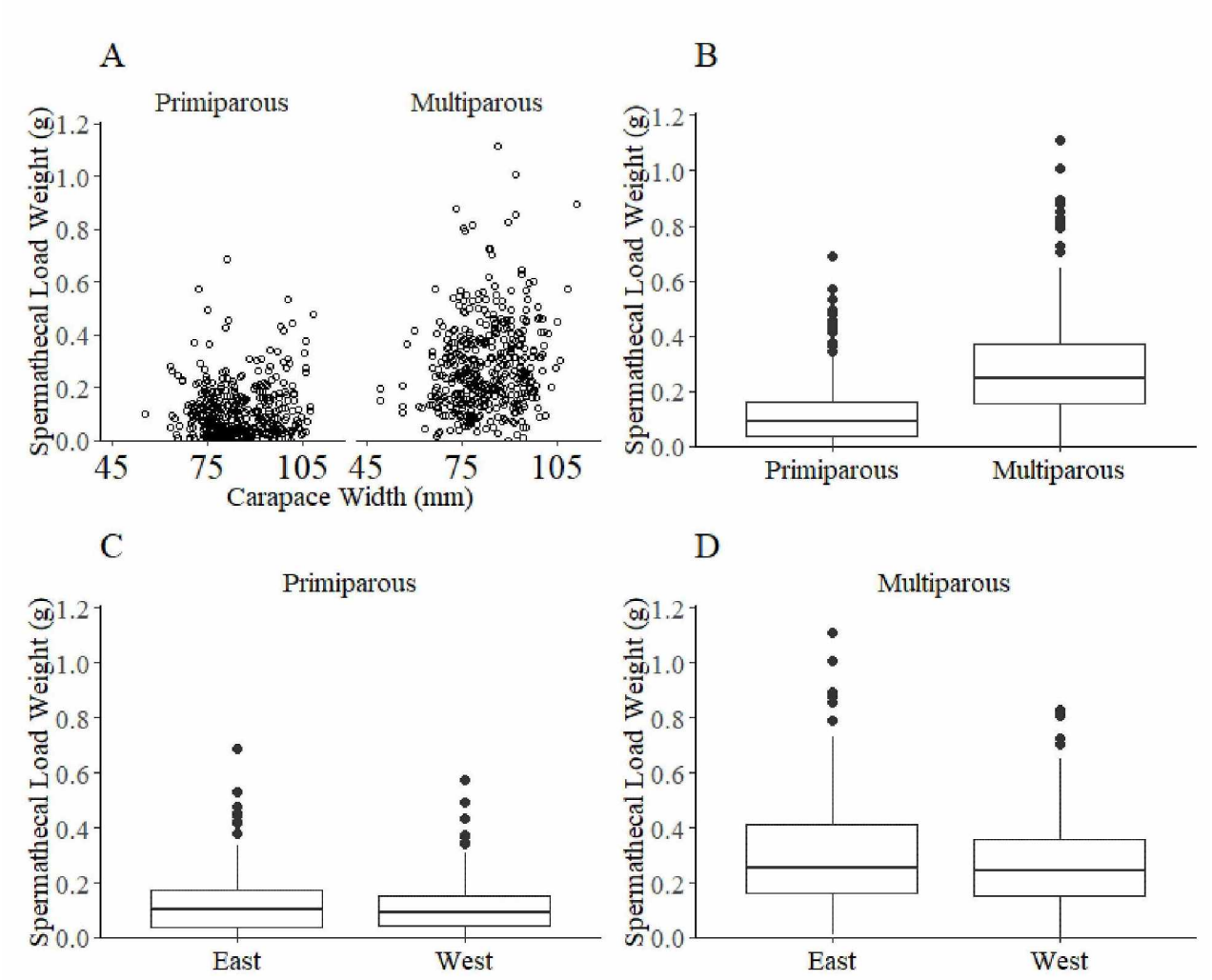

Figure 4. Spermathecal load (g) for females from the Eastern Bering Sea. Panel A is a scatterplot of raw data. Boxplots in panels B-D represent median value as middle line of the box with bottom and top of box representing 1st and 3rd quartiles. Outliers represented as black dots. There was insufficient evidence to conclude that spermathecal load (g) is directly related to female carapace width (panel A, $p=0.810$ for primiparous crab and 0.393 for multiparous crab); however, spermathecal load was significantly lower in primiparous females than in multiparous females (panel B, $p<0.001$). There was no difference detected in spermathecal load between the area east of longitude 166 °W longitude than in the area to the west for primiparous crab (panel C, $p=0.786$) but spermathecal load was lower in the west for multiparous crab (panel D, $p=0.034$).

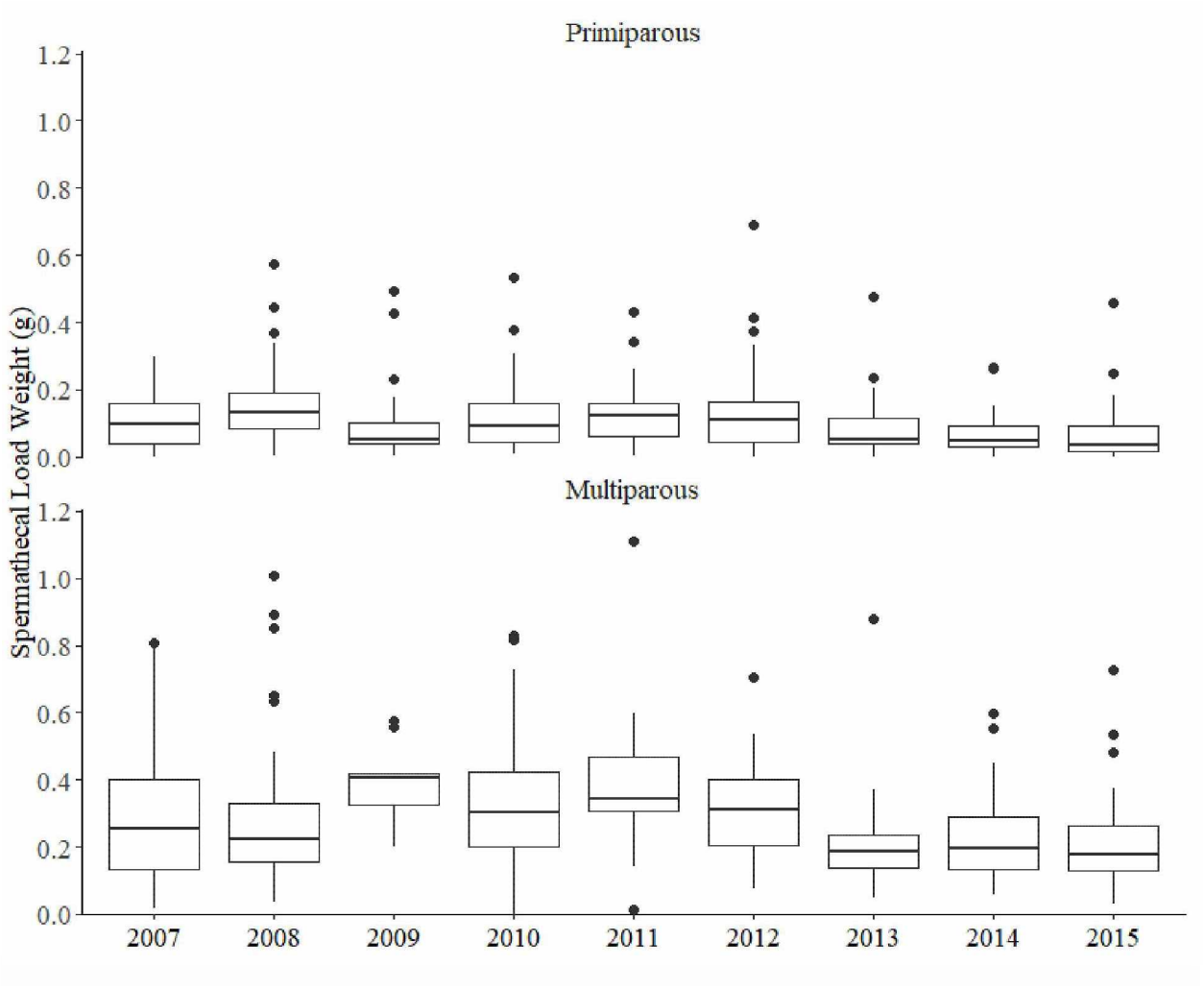

Figure 5. Spermathecal load (g) through time. There was a slight decrease detected in spermathecal load through time in primiparous females (p=0.033); however, there was insufficient evidence to detect the same pattern in multiparous females (p=0.455).

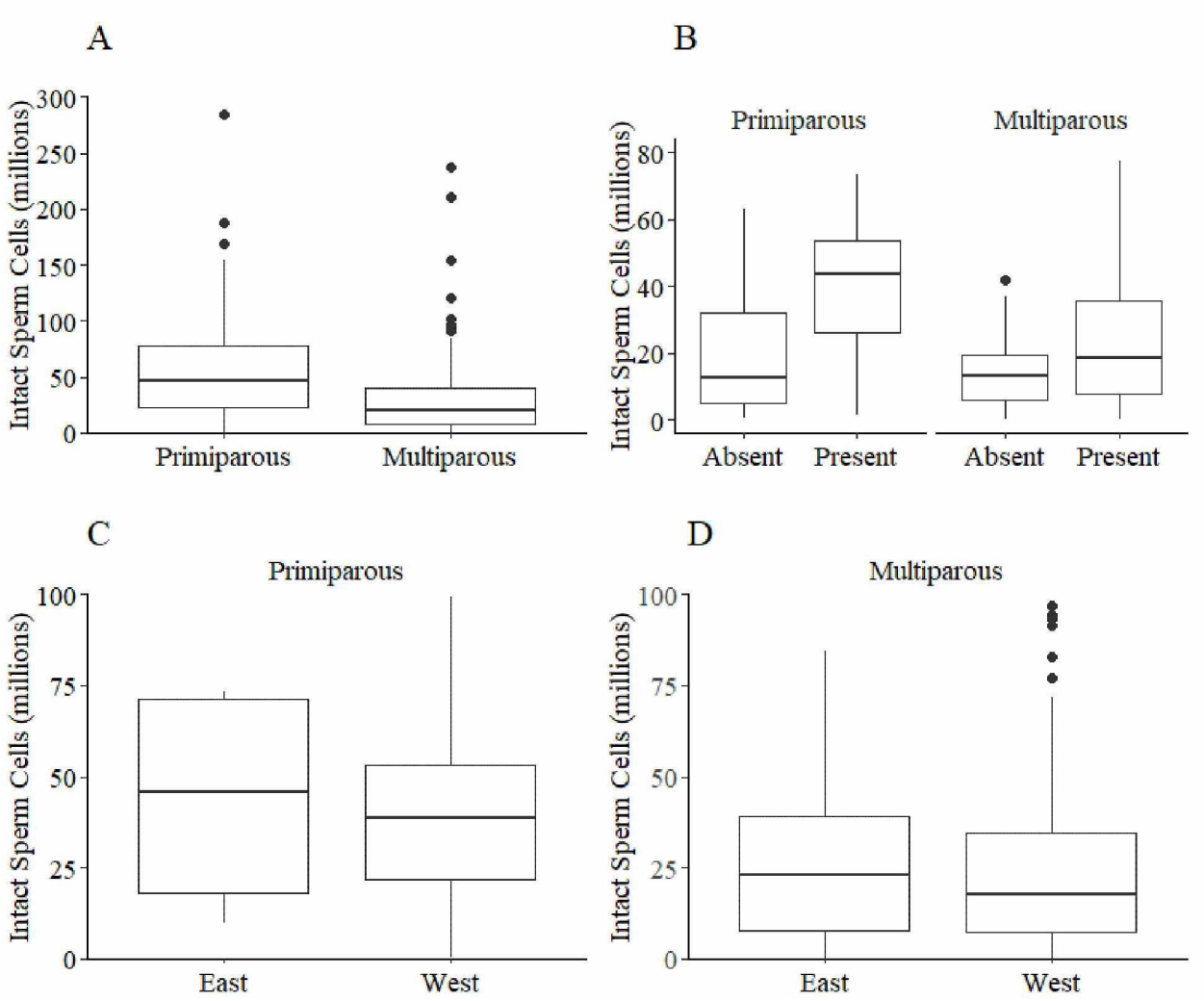

Figure 6. Sperm cell count (millions of cells) stored in the spermathecae of females from the Eastern Bering Sea. A) Sperm cell count was higher in primiparous crab than in multiparous crab ($p<0.001$). B) Sperm cell count was higher in primiparous females with visually confirmed presence of fresh ejaculate than in females without ($p<0.001$). The relationship did not hold for multiparous females ($p=0.075$). C) Primiparous sperm cell count was lower west of 166 °W longitude than east ($p=0.011$). D) Multiparous female sperm cell count did not vary east and west of 166 °W longitude ($p=0.838$).

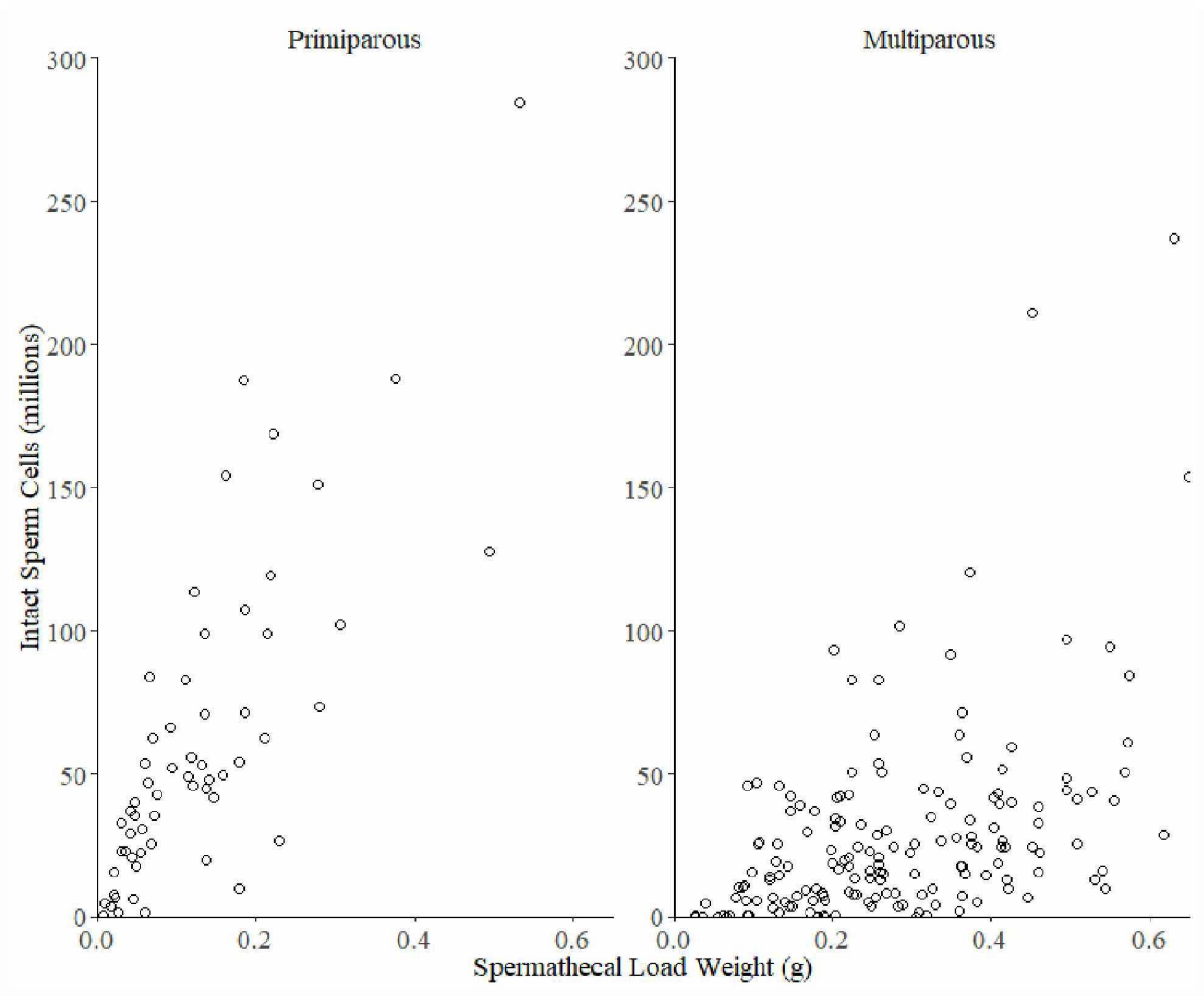

Figure 7. Relationship between spermathecal load (g) and sperm cell count (millions) by reproductive stage. The relationship is significant for primiparous and multiparous crab ($p<0.001$), although the slope of the regression is not the same for the two reproductive stages.

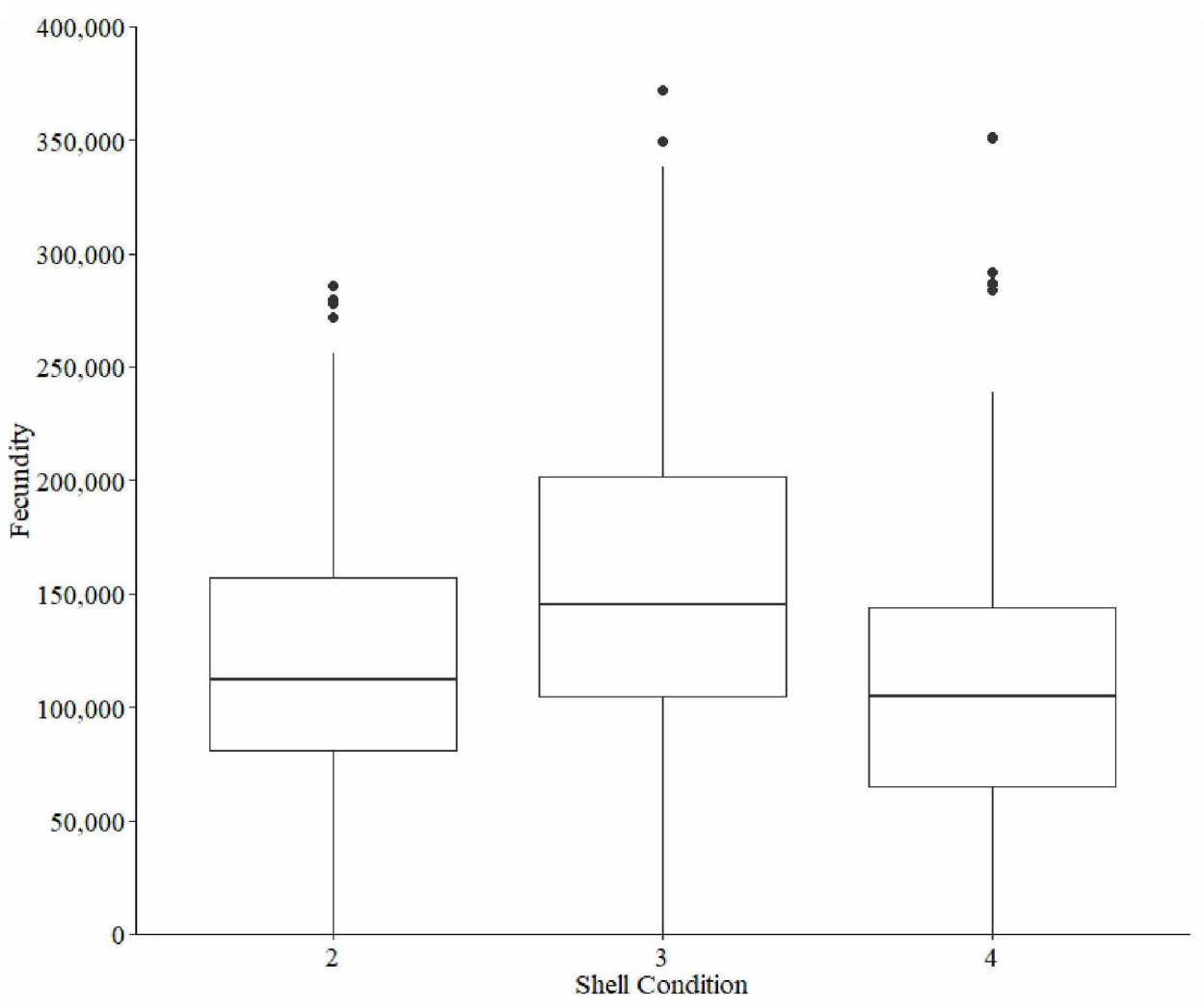

Figure 8. Relationship between female fecundity and female shell condition. Fecundity increased significantly between shell condition 2 and shell condition 3 crab ($p<0.001$) and decreased significantly between shell condition 3 and shell condition 4 crab ($p<0.001$). No difference in fecundity was detected between shell condition 2 and shell condition 4 crab ($p=0.959$).

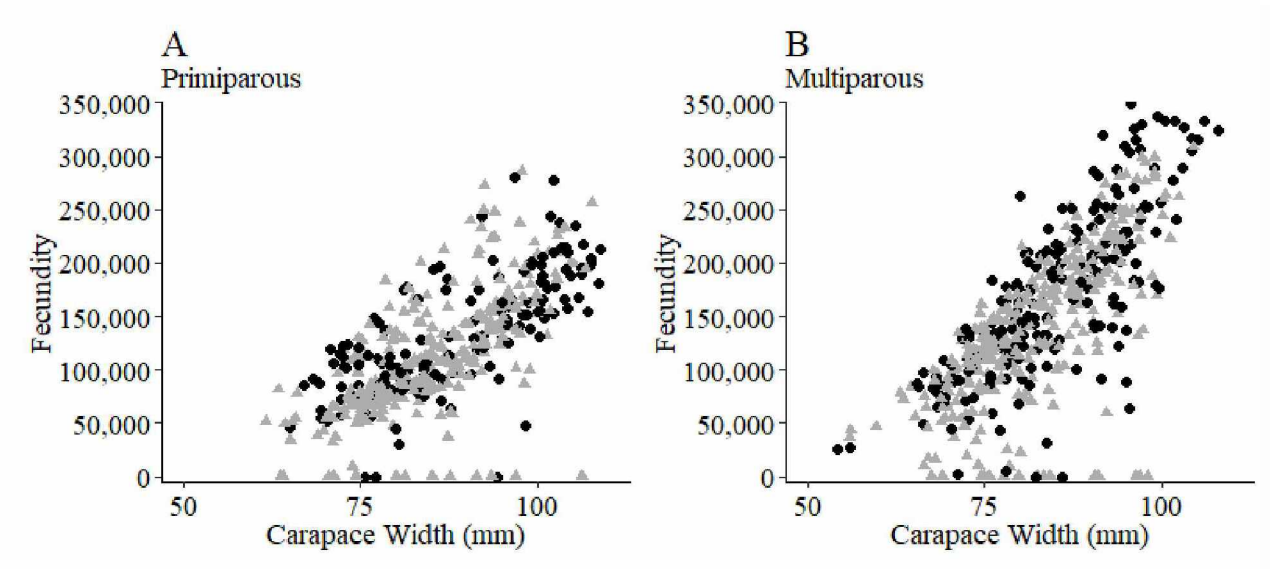

Figure 9. Female fecundity at size by region and reproductive stage. No difference in the probability of a female producing a clutch or the number of embryos produced for a given size were detected between A) primiparous crab to the east (black circles) and primiparous crab to the west (light grey triangles) of longitude 166°W (binomial component: p=0.840; Gaussian component: p=0.802). Likewise, no difference in the probability of a female producing a clutch or the number of embryos produced for a given size was detected between B) multiparous crab to the east and multiparous crab to the west of longitude 166°W (binomial component: p=0.181; Gaussian component: p=0.138).

Appendix

Table A1. Results of linear mixed model analysis of variation in primiparous female spermathecal load with the effect of female size (carapace width) and Area east and west of longitude 166 °W. Female collection location (station) and year estimated as random intercept-varying components of the model.

Spermathecal load (primiparous)					
$SL^{1/3} = \alpha + a_i + a_t + \beta CW + \delta Area + \varepsilon$					
n	Cond. R^2				
397	0.203				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	0.419	0.079	216.5	5.297	<0.001
Carapace width (β)	0.000	0.001	239.0	0.241	0.810
Area (West; δ)	0.006	0.024	57.3	0.272	0.786
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	0.0035	0.0589		
Year (a_t)	Random Intercept	0.0011	0.0332		
Residual (ε)		0.0179	0.1339		

Table A2. Results of linear mixed model analysis of variation in multiparous female spermathecal load with the effect of female size (carapace width) and Area east and west of longitude 166 °W. Female collection location (station) and year estimated as random intercept-varying components of the model.

Spermathecal load (multiparous)					
$SL^{1/3} = \alpha + a_i + a_t + \beta CW + \delta Area + \varepsilon$					
n	Cond. R^2				
424	0.388				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	0.618	0.067	312.3	9.203	<0.001
Carapace width (β)	0.001	0.001	408.7	0.855	0.393
Area (West; δ)	-0.057	0.026	62.9	-2.170	0.034
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	0.0059	0.0770		
Year (a_t)	Random Intercept	0.0018	0.0419		
Residual (ε)		0.0134	0.1159		

Table A3. Results of linear mixed model analysis of variation in primiparous female spermathecal load over time (year as continuous variable). Female collection location (station) estimated as random intercept-varying component of the model.

Spermathecal load (primiparous continuous year)					
$SL^{1/3} = \alpha + a_i + \beta Year + \varepsilon$					
n	Cond. R^2				
397	0.162				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	15.220	6.903	249.8	2.205	0.028
Year (β)	-0.007	0.003	249.7	-2.141	0.033
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	0.0033	0.0572		
Residual (ε)		0.0187	0.1368		

Table A4. Results of linear mixed model analysis of variation in multiparous female spermathecal load over time (year as continuous variable). Female collection location (station) estimated as random intercept-varying component of the model.

Spermathecal load (multiparous continuous year)					
$SL^{1/3} = \alpha + a_i + \beta Year + \varepsilon$					
n	Cond. R^2				
424	0.322				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	5.171	6.080	329.0	0.850	0.396
Year (β)	-0.023	0.003	329.0	-0.748	0.455
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	0.0066	0.0815		
Residual (ε)		0.0141	0.1186		

Table A5. Results of linear mixed model analysis of variation in female spermathecal load with the effect of ontogeny. Female collection location (station) and year estimated as random intercept-varying components of the model.

Spermathecal load and reproductive stage					
$SL^{1/3} = \alpha + a_i + a_t + \gamma RS + \varepsilon$					
n	Cond. R^2				
821	0.486				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	0.626	0.017	16.4	37.460	<0.001
Ontogeny (primip; γ)	-0.183	0.114	732.0	-16.020	<0.001
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	0.0054	0.0735		
Year (a_t)	Random Intercept	0.0014	0.0375		
Residual (ε)		0.0161	0.1267		

Table A6. Results of linear mixed model analysis of variation in female sperm cell count with the effect of ontogeny. Female collection location (station) estimated as random intercept-varying component of the model.

Sperm cell count and reproductive stage					
$SCC^{1/3} = \alpha + a_i + \gamma RS + \varepsilon$					
n	Cond. R^2				
277	0.176				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	258.120	10.860	38.9	23.778	<0.001
Ontogeny (primip; γ)	72.100	19.320	114.3	3.732	<0.001
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	1731.00	10.86		
Residual (ε)		12522.00	111.90		

Table A7. Results of linear mixed model analysis of variation in female sperm cell count with the effect of area east and west of longitude 166 °W and visual presence of fresh ejaculate in the spermathecae. Female collection location (station) estimated as random intercept-varying component of the model.

Sperm cell count (primiparous)					
$SCC^{1/3} = \alpha + a_i + \delta Area + \partial FE + \varepsilon$					
n	Cond. R^2				
61	0.438				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	307.860	44.650	44.2	6.895	<0.001
Area (δ)	-113.830	41.860	29.2	-2.719	0.011
Fresh Ejac Presence (∂)	184.060	30.070	51.0	6.122	<0.001
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	167.40	12.94		
Residual (ε)		10345.20	101.71		

Table A8. Results of linear mixed model analysis of variation in female sperm cell count with the effect of area east and west of longitude 166 °W and visual presence of fresh ejaculate in the spermathecae. Female collection location (station) estimated as random intercept-varying component of the model.

Sperm cell count (multiparous)					
$SCC^{1/3} = \alpha + a_i + \delta Area + \partial FE + \varepsilon$					
n	Cond. R^2				
169	0.151				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	237.443	30.344	66.1	7.825	<0.001
Area (δ)	-5.399	26.098	27.2	1.790	0.838
Fresh Ejac Presence (∂)	44.283	24.740	167.2	-0.207	0.075
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	1663.00	40.78		
Residual (ε)		10612.00	103.01		

Table A9. Results of mixed model analysis of the relationship of variation in primiparous female sperm cell count with spermathecal load. Female collection location (station) estimated as random intercept-varying component of the model.

Spermathecal load/sperm cell count relationship (primiparous)					
$SCC^{1/3} = \alpha + a_i + \beta SL^{1/3} + \varepsilon$					
n	Cond. R^2				
61	0.657				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	-6.659	34.322	61.0	-0.194	0.847
Spermathecal load (β)	768.955	71.719	61.0	10.722	<0.001
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	0.00	0.00		
Residual (ε)		6339.00	79.62		

Table A10. Results of mixed model analysis of the relationship of variation in multiparous female sperm cell count with spermathecal load. Female collection location (station) estimated as random intercept-varying component of the model.

Spermathecal load/sperm cell count relationship (multiparous)					
$SCC^{1/3} = \alpha + a_i + \beta SL^{1/3} + \varepsilon$					
n	Cond. R^2				
169	0.292				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	-9.451	38.574	106.8	-0.245	0.807
Spermathecal load (β)	431.318	58.288	125.6	7.400	<0.001
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	429.90	20.73		
Residual (ε)		8803.30	93.83		

Table A11. Results of binomial component of mixed model analysis of variation in primiparous female fecundity with the effect of female size (carapace width) and area east and west of longitude 166 °W. Female collection location (station) and year estimated as random intercept-varying component of the model.

Clutch production probability (primiparous)				
$log(\frac{p}{1-p}) = \alpha + a_i + a_t + \beta CW + \gamma Area + \varepsilon$				
n				
443				
Fixed Effects				
	Estimate	SE	z value	p
Intercept (α)	19.779	11.917	1.660	0.097
Carapace width (β)	0.000	0.081	0.005	0.996
Area (West; γ)	-0.747	3.706	-0.202	0.840
Components of residual variance				
	Type	Variance	SD	
Station (a_i)	Random Intercept	279.83	16.73	
Year (a_t)	Random Intercept	38.78	6.23	

Table A12. Results of Gaussian component of mixed model analysis of variation in primiparous female fecundity with the effect of female size (carapace width) and area east and west of longitude 166 °W. Female collection location (station) and year estimated as random intercept-varying component of the model.

Embryo production (primiparous)					
$fecundity^{1/2} = \alpha + a_i + a_t + \beta CW + \gamma Area + \varepsilon$					
n	Cond. R^2				
427	0.737				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	-178.580	26.988	282.7	-6.617	<0.001
Carapace width (β)	6.044	0.289	329.5	20.929	<0.001
Area (West; γ)	-2.313	9.153	52.4	-0.253	0.802
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	710.20	26.65		
Year (a_t)	Random Intercept	90.40	9.51		
Residual (ε)		1709.60	41.35		

Table A13. Results of binomial component of mixed model analysis of variation in multiparous female fecundity with the effect of female size (carapace width) and area east and west of longitude 166 °W. Female collection location (station) and year estimated as random intercept-varying component of the model.

Clutch production probability (multiparous)				
$log(\frac{p}{1-p}) = \alpha + a_i + a_t + \beta CW + \gamma Area + \varepsilon$				
n				
523				
Fixed Effects				
	Estimate	SE	z value	p
Intercept (α)	4.965	2.963	1.676	0.094
Carapace width (β)	0.014	0.034	0.416	0.677
Area (West; γ)	-1.396	1.044	-1.334	0.181
Components of residual variance				
	Type	Variance	SD	
Station (a_i)	Random Intercept	2.50	1.58	
Year (a_t)	Random Intercept	1.43	1.20	

Table A14. Results of Gaussian component of mixed model analysis of variation in multiparous female fecundity with the effect of female size (carapace width) and area east and west of longitude 166 °W. Female collection location (station) and year estimated as random intercept-varying component of the model.

Embryo production (multiparous)					
$fecundity^{1/2} = \alpha + a_i + a_t + \beta CW + \gamma Area + \varepsilon$					
n	Cond. R^2				
505	0.718				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	-208.832	26.280	177.3	-7.947	<0.001
Carapace width (β)	7.153	0.275	395.1	26.039	<0.001
Area (West; γ)	-12.249	8.105	41.2	-1.511	0.138
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	420.90	25.52		
Year (a_t)	Random Intercept	893.30	29.89		
Residual (ε)		2611.10	51.10		

Table A15. Results of binomial component of mixed model analysis of variation in female fecundity with the effect of female size (carapace width) and reproductive stage (shell condition). Female collection location (station) and year estimated as random intercept-varying component of the model.

Clutch production probability by shell condition				
$log\left(\frac{p}{1-p}\right) = \alpha + a_i + a_t + \beta CW + \gamma SC + \varepsilon$				
n				
1153				
Fixed Effects				
	Estimate	SE	z value	p
Intercept (α)	2.193	2.163	1.014	0.311
Carapace width (β)	0.039	0.024	1.637	0.102
SC (3; γ)	0.418	0.485	0.862	0.389
SC (4; γ)	0.696	0.693	1.005	0.315
Components of residual variance				
	Type	Variance	SD	
Station (a_i)	Random Intercept	2.37	1.54	
Year (a_t)	Random Intercept	3.21	1.79	

Table A16. Results of Gaussian component of mixed model analysis of variation in female fecundity with the effect of female size (carapace width) and reproductive stage (shell condition). Female collection location (station) and year estimated as random intercept-varying component of the model.

Embryo production by shell condition					
$fecundity^{1/2} = \alpha + a_i + a_t + \beta CW + \gamma SC + \varepsilon$					
n	Cond. R^2				
1113	0.622				
Fixed Effects					
	Estimate	SE	df	t value	P
Intercept (α)	-190.391	19.480	402.8	-9.773	<0.001
Carapace width (β)	6.102	0.212	878.8	28.797	<0.001
SC (3; γ)	54.442	4.469	1007.9	12.182	<0.001
SC (4; γ)	0.345	6.780	893.1	0.051	0.959
Components of residual variance					
	Type	Variance	SD		
Station (a_i)	Random Intercept	675.60	25.99		
Year (a_t)	Random Intercept	344.60	18.56		
Residual (ε)		3102.70	55.70		